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RHIPIDISTIAN CLASSIFICATION IN RELATION TO THE ORIGIN OF THE TETRAPODS

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INTRODUCTION

In an extensive study of the nasal region of the lower gnathostomes, Jarvik (1942) concluded that the four families of rhipidistian Crossopterygii represent two distinct stocks (superorders according to Lehman, 1959) — the 'Porolepiformes' (Porolepidae and Holoptychidae) and the 'Osteolepiformes' (Osteolepidae and Rhizodontidae). Of major interest to students of vertebrate evolution was his conclusion that the structures seen in the snout of 'Porolepiformes' were closely comparable to those seen in the recent Urodela, and those of 'Osteolepiformes' were comparable to those of the recent *Anura*, and that here was evidence of a biphyletic origin of the tetrapods. His work was based upon detailed studies of two genera, *Porolepis* and *Eusthenopteron* (a rhizodontid). Jarvik's material was unusual in that it showed details of the endocranial part of the snout which it is not usually possible to study in fossil crossopterygians; in recent years, however, more such material has been described (Vorobjeva, 1959, 1960a, 1960b; Kuleyzeki, 1960) and Ørvig (1957) has published a full treatment of the interrelations of the Rhipidistia on the basis of the structure of the scales. For the last year or so I have been engaged in a study of the ethmoid region of the osteolepids *Megalichthys* and *Ectosteorhachis*, continuing the work started by Romer (1937, 1941).

Briefly, the newly available evidence does not support all of Jarvik's original conclusions. Because of the relation of this

work to the problem of the origin of the tetrapods and particularly to the currently disputed theories of the ancestry of the recent Amphibia, I have decided to publish this short review of the more pertinent points in advance of a more thorough treatment. This may also be useful since the work of Vorobjeva, being in Russian, may not be readily available to everyone.

This paper forms part of the work to be submitted to the Department of Biology, Harvard University, in fulfillment of the requirements for the degree of Doctor of Philosophy; it is my pleasure to acknowledge the constant help and guidance of Professor A. S. Romer during all this study; he and Dr. E. E. Williams and Professor B. Patterson read and criticized the manuscript. I am also grateful for the friendly encouragement of Drs. Jarvik and Örvig in Stockholm; the former has allowed me to see an as yet unpublished manuscript on this subject (Jarvik, in press). My friend Mr. Simon Karlinsky provided the translations from the Russian. My studies have been supported by the award of N.A.T.O. Science Studentship 3/60/955 by H. M. Department of Scientific and Industrial Research, London, and by the Jeffries Wyman Scholarship at Harvard University.

MATERIAL

It is necessary to establish the taxonomic status of certain of the rhipidistians concerned in this study; these are:

Megalichthys Agassiz 1841 (including *Ectosteorhachis* Cope 1880). Carboniferous and Lower Permian of Europe and North America.

Platycephalichthys Vorobjeva 1959. Upper Devonian of U.S.S.R.

Panderichthys Gress 1941. Upper Devonian of U.S.S.R.

Porolepis (*P. ex grege posnaniensis* [Kade 1858]). Lower Devonian of Poland.

Megalichthys-Ectosteorhachis. *Ectosteorhachis* was originally described by Cope (1880) from material from the Lower Permian of Texas; it was later (1891) referred by him to the Carboniferous genus *Megalichthys*. In recent years it has been suggested several times (see, for example, Romer, 1941) that the two genera are, in fact, distinct and that the Lower Permian material will have to be referred back to *Ectosteorhachis*. No formal diagnosis of this has been given; however, in advance of

such a diagnosis I shall follow precedent and refer to the Permian fish, for convenience, as '*Ectosteorhachis*.'

Megalichthys and *Ectosteorhachis* are generally acknowledged to be members of the Osteolepidae. Berg (1958) unites them with Owen's *Parabatrachus* to form the separate family Parabatrachidae; however, available evidence, e.g. Bystrow (1950), shows that *Megalichthys* is closely related to *Osteolepis* itself.

Porolepis. Kulezycki's (1960) material of *Porolepis* is without doubt correctly referred to that genus.

Platycephalichthys and *Panderichthys*. These genera are involved in a long series of taxonomic shufflings concerning the genera *Cricodus*, *Dendrodus* and *Polycodus*; they may be considered most conveniently together. The best way to review the situation seems to be to start with the description by Rohon (1889) of several specimens from the Upper Devonian of Russia, some of which he assigned to *Dendrodus biporcatus* Owen (Rohon, 1889, plate 1, figures 1, 5, 9, a skull, and 2, 7 8, a tooth and two scales), while others he named *Cricodus wenjucovi* (Rohon, 1889, plate 1, figures 4, 6, a skull from the River Ojatj, and 3, 11, a skull and lower jaw from the River Sjass). Since these specimens are not given numbers by Rohon, I shall refer to them, for convenience, by the number of the figure by which they are illustrated.

Gross (1933) placed those specimens figured in plate 1, figures 1, 3, 4, 5, 6, 9, together with new material from the Baltic Old Red Sandstone, in the genus *Polyplacodus* Pander 1860, as the new combination *Polyplacodus wenjucovi*. Jarvik (1937), however, put "figures 1, 3, 4, 5, 6, 9, 11" in *Eusthenopteron* as *E. wenjucovi*. He also concluded that the names *Cricodus*, *Dendrodus*, and *Polyplacodus* should not be assigned to any fresh material because of the fragmentary and enigmatic nature of the originals. Hence Gross (1941) named a new genus *Panderichthys* in order to reassign material named by him (1930) *Polyplacodus* (*Cricodus*) *rhombolepis* (see also Gross 1933, 1936). Now there enters a possible source of confusion because Gross (1941) named a second new species — *Panderichthys bystrovi* — for the material from the Baltic Old Red which he had named *Polyplacodus wenjucovi* in 1933 (see above), while leaving the Rohon material in *Eusthenopteron wenjucovi*. Vorobjeva (1960a) named a third species — *Panderichthys stolbovi*.

In 1959 Vorobjeva described a new genus *Platycephalichthys*, with the type *Platycephalichthys bischoffi*, based on recently collected material from the Upper Devonian of Russia, and included in this genus the Rohon specimen from River Ojatj ("figures 4 and 6") as a new species *Platycephalichthys rohani*. Later (1960b) she referred the remaining Rohon material to *Eusthenodon* Jarvik 1955 as *Eusthenodon wenjucovi*.

Thus the two genera now comprise:

Panderichthys

P. rhombolepis Gross 1941

P. bystrovi Gross 1941

P. stolbovi Vorobjeva 1960

Platycephalichthys

P. bischoffi Vorobjeva 1959

P. rohani Vorobjeva 1959

From the structure of the scales and teeth, *Platycephalichthys* is a member of the Rhizodontidae. *Panderichthys* was assigned by Gross (1941) to the Rhizodontidae but there seems little doubt (Vorobjeva 1960a, and Ørvig 1957) that it should be placed with the Osteolepidae.

SUBDIVISION OF THE RHIPIDISTIA

Jarvik (1942, p. 489) lists a series of differences between *Porolepis* and *Eusthenopteron* which he considers to be representative of a basic split within the Rhipidistia. He also (1942, pp. 417, 495) discusses the connections between these fishes and the recent Amphibia. In general, the same characters are involved in the two arguments. In the next few pages I shall review recent findings which indicate that certain of these characters no longer support Jarvik's distinctions. These are all characters which may readily be determined in the fossils; this is in contrast with some of Jarvik's points involving the passage of nerves and vessels, the refutation of which could be as difficult as their interpretation. Some of Kulczycki's (1960) statements may be disputed, as I shall mention later, on the grounds that his material was insufficiently well preserved. This criticism cannot apply to Vorobjeva's work, particularly since the most important of the characters she has described are, as already mentioned, easily ascertained.

The recognition, in certain anatomical characters, of resemblances between specific rhipidistians and recent amphibians, without the supporting evidence of a fossil lineage (lacking in

the case of the Urodela and Anura) becomes, to a certain extent, a matter of subjective judgment. In the following pages I shall consider primarily the evidence for a basic distinction between 'Osteolepiformes' and 'Porolepiformes,' for it is upon the validity of this supposed dichotomy that all subsequent phylogenetic hypothesis must rest.

The nature of the anterior palatal fenestrae. According to Jarvik (1942, p. 489, etc.), an important difference between the 'Osteolepiformes' and the 'Porolepiformes' lies in the nature of the paired palatal recesses present between the anterior edges of the vomers and the posterior rim of the premaxillae. In *Eusthenopteron* this region has the form of a shallow, partially sub-divided groove, the 'prenasal groove,' limited posteriorly by the edges of the vomers; in *Porolepis* there is a pair of 'pits' extending backwards between and separating the vomers. These palatal recesses which are described by three names — 'fossae apicales,' 'anterior palatal fenestrae,' and 'pre-nasal pits' — were assumed by Jarvik to have contained glandular organs homologous with the various intermaxillary glands of recent Amphibia. It was further proposed that the condition in *Eusthenopteron* foreshadowed that of recent Anura, and the condition in *Porolepis* that of Urodela.

It had already been suggested, however, that these recesses served solely to receive the points of large tusk-like teeth set in the tips of the lower jaws (Holmgren and Stensiö, 1936; Romer, 1937; and now also Kuleczycki, 1960). The material at my disposal shows quite clearly that this latter explanation is the true one for the Osteolepidae. Plate I shows the tusk fitting into the palatal recess, leaving no room for any glandular structure. That this is also the case in other 'Osteolepiformes' may be deduced from the similar large tusks of the lower jaws — for example, in *Panderichthys* (Gross, 1941). In 'Porolepiformes' the situation is very similar, but in this case, as Jarvik has shown, the teeth concerned are a pair of tooth whorls. This extremely interesting discovery provides, incidentally, positive indication that the familiar *Onychodus*, long known from such tooth whorls, is, in fact, a 'porolepiform' rhipidistian (Jarvik, in press).

The presence of the paired tooth whorls speaks, indeed, for the unity of the 'Porolepiformes,' but the morphological relationship between the type of palatal fenestra and the lower jaw dentition completely precludes any phylogenetic relationship

between the fenestrae in Rhipidistia and the glandular organs of recent Amphibia.

Evidence from the cranial cavity. A point of resemblance, apparently possible of interpretation as evidence of relationship, between *Porolepis* and the Urodela is that in both “. . . the internasal wall is broad and does not form any nasal septum. It lodges the ethmoid part of the cranial cavity” (Jarvik, 1942, p. 417). This, moreover, is supposed to be in direct contrast with the ‘Osteolepiformes’ (and Anura) — by extrapolation from the situation in *Eusthenopteron* in which the internasal wall is relatively narrow and also solid.

Kuleyzeki (1960) noted that his material of *Porolepis* did not show any forward extension of the cranial cavity between the nasal sacs; his material was perhaps not as good as might be desired fully to substantiate this view, since it consisted entirely of natural casts and not true bony remains. At the same time that Kuleyzeki’s work was published there appeared the work of Vorobjeva. Her material consisted of several portions of the skulls of *Platycephalichthys* and *Panderichthys*, both of which are undoubtedly ‘osteolepiform’ and both of which, she states, have an ethmoid extension of the cranial cavity. Her description of *Platycephalichthys* is interesting; “. . . a wide internasal portion (of the braincase) with a cavity stretching forward almost to the front edge of the skull” (Vorobjeva, 1960a, trans.).

In the face of evidence that a rhizodontid and an osteolepid have a ‘pars ethmoidalis cranialis’ and at least one species of *Porolepis* may not, one is forced to conclude that this character is of no significance in any attempt to distinguish supra-familial groupings within the Rhipidistia. One may further bear in mind that the extent of the cranial cavity need have no relation to the extent of the brain contained therein. A dramatic demonstration of this is afforded by the coelacanth *Latimeria* (Millot and Anthony, 1958), in which a large cranial cavity contains but a small brain. Presence or absence of the pars ethmoidalis cranialis is thus a rather labile character in the Rhipidistia and, having no great anatomical or functional basis, no phylogenetic speculation may reasonably be drawn from it.

Nasal apertures and the nasal cavity. All known ‘Porolepiformes’ are characterized by the presence of two external nares and a choana. Further, the endocranial opening for the posterior naris is confluent with that for the choana. In *Eusthenopteron*, on the other hand, there is but one external naris and this

is separated from the choana by the lamina nario-choanalis of the endoskeletal nasal capsule. Until the work of Vorobjeva this was believed to hold true for all 'Osteolepiformes' but *Panderichthys* is described (Vorobjeva, 1960a) as having both an anterior and a posterior external naris. From her figures it is not possible to determine whether the described confluence of the posterior naris with the fenestra endochoanalis is due merely to a defect in the preservation or not. This is indeed a strange situation for a fish which is in all major respects to be considered 'osteolepiform.'

Jarvik has other speculations based on the detailed configuration of the nasal cavity itself, but these seem to be more open to dispute in connection with phylogenies spanning 300 million years. *Ectosteorhachis* certainly lacks most of the ridges, grooves and depressions described in *Eusthenopteron* and supposed to be typical of all 'Osteolepiformes.'

Jarvik described in *Eusthenopteron* a foramen in the post-nasal wall which he states is the posterior endonarinal fenestra (Jarvik's terminology). This is also present in *Ectosteorhachis*, but the presence of an anterior naris in *Panderichthys* may possibly indicate that the single external naris of 'Osteolepiformes' is homologous with the posterior naris of *Porolepis*. In this case the foramen in the post-nasal wall, which Jarvik considers to be the forerunner of the tetrapod naso-lachrymal duct, may possibly have to be interpreted in some other fashion, but considerably more evidence is needed to settle this point.

Other structures. There are several other points, noted by Jarvik as indicative of a division within the Rhipidistia, which are contradicted by the anatomy of *Ectosteorhachis*:

1) Jarvik (1942, p. 492) states that a difference between 'Osteolepiformes' and 'Porolepiformes' is that in the former the vomers are in mesial contact, while in the latter they are separate from each other. Although in the sectioned material at my disposal the vomers are slightly displaced, it seems that these bones are not in mesial contact. Further, they lack the posterior extension passing back on either side of the tooth-bearing part of the parasphenoid, which has also been stated to be typical of 'Osteolepiformes.' The vomers are thus much more similar to those of *Porolepis* than to those of *Eusthenopteron*; they lie entirely anterior to the tooth-bearing part of the parasphenoid.

2) Jarvik states (1942, p. 492) that in 'Osteolepiformes' the parasphenoid is narrow and in 'Porolepiformes' it is broad. But in *Ectosteorhachis* (an osteolepid) only the tooth-bearing part is narrow — the parasphenoid is continued forward and laterally as a broad, if thin, film of bone fused to the ventral surface of the endocranium (cf. Romer, 1937, p. 19).

3) Jarvik states that lack of the external parietal foramen is typical only of 'Porolepiformes'; both *Megalichthys* and *Ectosteorhachis* lack it, however.

Kuleyzeki further criticizes Jarvik's description of the snout anatomy of *Porolepis*, especially the detailed description of the nasal capsule and the canals for nerves and vessels (see especially Kuleyzeki, 1960, pp. 81-94). On the other hand, Jarvik states (in press) that in most details the new material he has of *Glyptolepis* fully bears out his description of *Porolepis*.

DISCUSSION AND CONCLUSIONS

The nature of the fossil remains, by which the Rhipidistia are known, is extremely variable, ranging from the excellent and fairly plentiful material preserved 'in the round' of *Eusthenopteron*, *Ectosteorhachis* and *Glyptolepis* (Jarvik, in press, and in preparation), to the fragments of skulls, isolated teeth, and scales typical of most genera. It is not surprising, therefore, that most phylogenies and taxonomic studies have been based on the histology of teeth and scales. The latter approach is, of course, open to some doubts and reservations, but the recent work of Ørvig seems particularly important (see Ørvig, 1957, p. 409 for phylogeny).

It is especially interesting to note the positions assigned by Ørvig to *Panderichthys* and *Platycephalichthys*. According to Jarvik's interpretations of crossopterygian anatomy, the presence of the pars ethmoidalis cranialis in both genera and the two external nares in *Panderichthys* would ally them with the *Porolepis* lineage. All other evidence, however (Ørvig and Vorobjeva), opposes this view and maintains their 'osteolepiform' status. One is forced to conclude that these two characters are more labile than was formerly supposed; they fail to show correlation with other, diagnostic, characters.

Schmalhausen (1959) rejected Jarvik's theories on the grounds that the two 'types' of skull merely reflected the relative proportions of the skull, *Porolepis* being broad-snouted and *Eusthenopteron* narrow-snouted. Schmalhausen was referring particularly to the difference between the two types of anterior

palatal fenestra, the nature of which we have already seen to depend on the type of lower jaw dentition. Although Schmalhausen's idea is an attractive one, it does not explain the discrepancy in the occurrence of the pars ethmoidalis cranialis. The 'Osteolepiformes' contain both broad and narrow snouted forms, but the presence of the pars ethmoidalis cranialis is independent of this factor:

		Pars ethmoidalis	
		Snout	cranialis
Osteolepidae	} <i>Ectosteorhachis</i> } <i>Panderichthys</i>	Broad	Absent
		Narrow	Present
Rhizodontidae	} <i>Eusthenopteron</i> } <i>Platycephalichthys</i>	Narrow	Absent
		Broad	Present

This character is not even related to the relative width of the internasal wall, which seems to be dependent on the relative size of the nasal capsules rather than on the external proportions or intrinsic 'osteolepiform'/'porolepiform' nature of the snout.

I can think of no explanation of the apparently random occurrence of these characters except that the Rhipidistia form a fairly close-knit group within which comparable variations can occur in all families.

There is no doubt that a distinction of some sort can be drawn between a porolepiform and an osteolepiform assemblage (although the former is a much more compact group than the latter). The controversy lies in the status to be assigned to each. The two groups have been interpreted by Jarvik (1942, 1955, 1960) to represent a fundamental split within the Rhipidistia and, by extrapolation, within the recent Amphibia also. There are two major objections to the arguments which are presented to substantiate this hypothesis. Firstly, only one genus of 'Osteolepiformes' (*Eusthenopteron*) was available for consideration in any detail, and secondly, all the characters dividing the two groups are chosen with reference to the proposed relation to the Urodela or Anura and not at all with reference to the Rhipidistia in general. Taking into consideration the evidence presented above and bearing in mind other more detailed points such as are disputed by Kuleyzecki and to which I hope to return in a future work, it seems that the two groups of Rhipidistia are more closely related than has been stated. Furthermore, those characters which might reflect a relationship with particular

recent Amphibia are present in both groups of rhipidistians and are not, therefore, justifiably so considered.

From my own studies of the Rhipidistia, I personally favour the view propounded by Berg (1958) that there are three groups of Rhipidistia: the Porolepiformes, the Osteolepiformes and the Rhizodontiformes. I would allow each group no more than super-familial rank.

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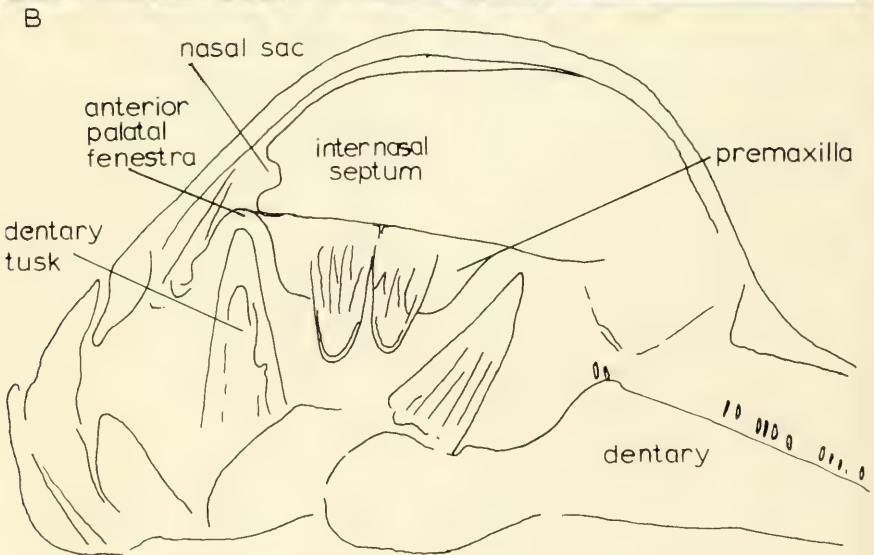
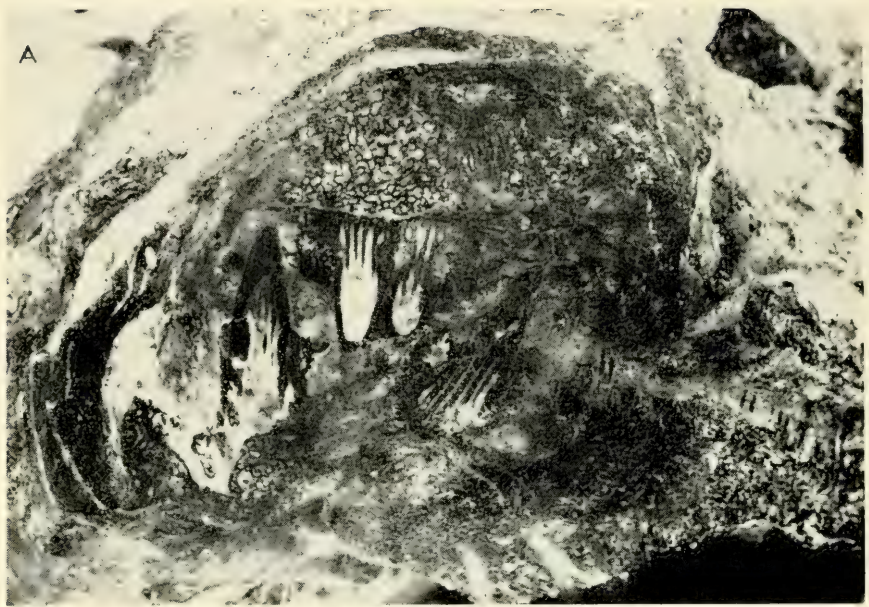


Plate 1.

Megalichthys from the Scottish Carboniferous. M.C.Z. 8941. Tip of the snout in anterior view, showing premaxillary teeth, dentary tusks, and the anterior palatal fenestrae exposed by a natural break in the specimen:

A. Photographed immersed in water.

B. Semi-diagrammatic sketch of A, emphasizing the pertinent features.